# Spatial Patterns and Drivers of Chinese Lizard Richness among Multiple Scales

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**Abstract** Species richness is one of the focuses of the preponderance of ecological studies. Latitudinal and altitudinal gradients of species richness are two well-known macroecological patterns. Most studies on the macroecology of species richness and its determinants are mainly focused on a single scale, although a few include multiple scales. Across multiple scales, we can better understand the diversity gradients and the potential causes. Here, we gathered the maps of distribution for 212 species of Chinese lizards from published studies, and to describe the overall Chinese lizard richness patterns. We studied the relationships between the latitudinal and altitudinal patterns of species richness among Chinese lizards at the assemblage level. We further tested the relationship between lizard richness and environmental factors among multiple studied scales (large scale: 1.5° × 1.5°, medium scale: 1° × 1°, and small scale: 0.5° × 0.5°). Regions with higher species richness occurs in in south China, and we found negative latitudinal richness gradients. We found a low-altitude plateau pattern between species richness and altitude, and lizard richness decreased with altitude above 2500 m. Lizard richness was positively correlated with temperature and net primary productivity, but negatively correlated with actual evapotranspiration, temperature, and precipitation seasonality at all three scales. However, lizard species richness was positively correlated with heterogeneity only at the 1° scale. Based on the results across multiple scales, we confirmed that the species richness patterns of Chinese lizards were driven by multiple factors, which consistent with the predictions of the ambient energy, seasonality, and productivity hypotheses. However, the relationship between lizard richness and heterogeneity differed among studied scales owing to the different levels of altitude heterogeneity within grids at different scales.

**Keywords** altitudinal, assemblage, diversity, environmental factors, latitudinal, reptile

## 1. Introduction

"The distribution of organisms is not random." —— [Carsten Rahbek, 1997].

Species richness is the number of species in a given area (Ricklefs, 2004). It is one of the focuses of the preponderance of ecological studies (Astudillo-Scalia and Albuquerque, 2020; Dillon and Conway, 2021; Huang *et al.*, 2011; Whiting and Fox, 2021; Zhang *et al.*, 2021). Therefore, recording and exploring the spatial pattern of species richness have been central topics of macroecology and biogeography since their origin.

Latitudinal and altitudinal gradients of species richness are two well-known macroecological patterns. The pattern that shows an overall decrease in species richness from the equator to the poles is referred to as the latitudinal gradient (Dobzhansky, 1950; Pianka, 1966). Similarly, the decrease in species richness with increasing altitude is widely accepted as a general pattern of altitudinal gradients (Rahbek, 1995). Moreover, altitudinal gradient has the following four detailed patterns (Rahbek, 1995; 1997): (1) decreasing richness with increasing altitude, (2) low-altitude plateau, (3) low-altitude plateau with a mid-altitude peak, and (4) mid-altitude peak (McCain, 2010, and Figure 1).
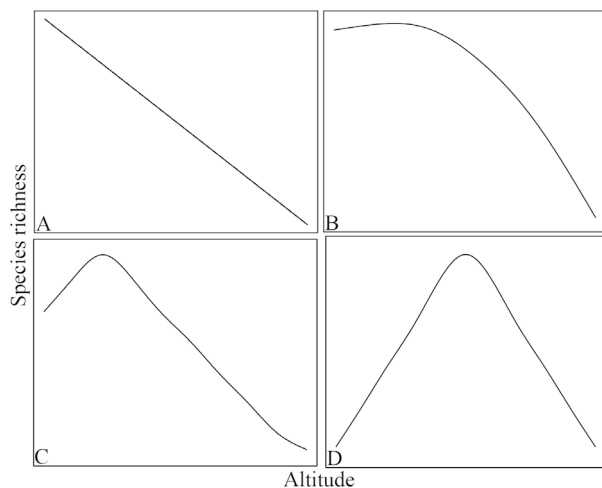
**Figure 1** Four detailed relationships between species richness and altitude described in previous studies (Rahbek, 1995; 1997). A: Decreasing; B: Low-altitude plateau; C: Low-altitude plateau with a mid-altitude peak; D: Mid-altitude peak.

There are many studies on the mechanistic drivers of spatial patterns in species richness among several taxa (such as mammals, birds, and reptiles). Climate is considered as a major driver of the broad geographical scaled patterns of species richness. multiple factors, such as temperature (Lewin *et al.*, 2016), precipitation (Currie, 1991), habitat heterogeneity (Hortal *et al.*, 2013), productivity (Evans *et al.*, 2005), altitude (Dillon and Conway, 2021), and latitude (Whiting and Fox, 2021), could shape the spatial patterns of—and cause variations in—species richness.

Similar to other ecological patterns, species richness patterns are also scale-dependent (Evans *et al.*, 2008). The determinants of richness pattern may differ with scale. This is true for reptiles; for example, net primary productivity played a stronger role (1° vs ecoregions) in shaping African reptile species richness at a finer scale (Lewin *et al.*, 2016). For European reptiles, precipitation was significantly correlated with species richness at a 0.5° scale (Whittaker *et al.*, 2007), However, at a 1° scale, precipitation was no longer correlated with species richness (Rodríguez *et al.*, 2005). Therefore, the spatial patterns of species richness formation, strength, and the underlying determinants vary with the scale. Thus, elucidating richness gradients and their determinants requires further study of their variations in relation to the spatial scale.

Understanding species richness patterns is a prerequisite for maintaining species diversity. Studies on reptiles, however, are relatively rare compared to those on other taxa, such as mammals and birds (Pollock *et al.*, 2017; Rosauer *et al.*, 2017). Reptiles are different from other terrestrial vertebrates because

their distributions usually show their adaptation to arid regions (Roll *et al.*, 2017). Reptile richness patterns are associated with ambient energy (Hawkins *et al.*, 2003; Qian *et al.*, 2007; Rodríguez *et al.*, 2005) and vary within specific lineages. For example, water and ambient energy can predict snake and turtle richness, while lizard richness is more correlated with energy (Hawkins *et al.*, 2003; Schall and Pianka, 1978; Terribile *et al.*, 2010). Increasing evidence suggests that species richness is driven by multiple factors (e.g., lizards, snakes, Huang *et al.*, 2011, Cai *et al.*, 2012).

China provides a good environment for studies on the spatial pattern of Chinese reptile species richness and its determinants. And Chinese reptile species richness has been well studied in the past 15 years (Huang *et al.*, 2011; Qian *et al.*, 2007; Zhao *et al.*, 2006). Huang *et al.* (2011) found that multiple factors explain Chinese lizard species richness at the assemblage level. However, this conclusion was based on a 100-km scale (~1°), and a detailed discussion of the underlying determinants of species richness across multiple scales is still lacking (Evans *et al.*, 2008).

In this study, in order to explore scale dependency in the influence of climatic factors among Chinese lizards, we gathered the maps of distribution for 212 species of Chinese lizards from published studies, and to describe Chinese lizard richness patterns. We focused on three different scales: 1.5° × 1.5° (large), 1° × 1° (medium), and 0.5° × 0.5° (small). We aimed to (1) explore the latitudinal and altitudinal richness gradients for Chinese lizards, (2) explore the spatial patterns of lizard species richness and the potential determinants among three scales, and (3) examine whether scale could influence climate–species richness correlations among Chinese lizards.

## 2. Material and methods

**2.1. Data collection**  A total of 212 species were included in this study, and these species represent 90% of Chinese lizard species (239 species, update to 2021-11, see Appendix S1). We obtained a distribution map of Chinese lizards for these 212 species, which from a recent paper (Liang *et al.*, 2021). Of these 212 species, we note that 165 species maps were from the Global Assessment of Reptile Distributions (GARD, http://www.gardinitiative.org/) (Roll *et al.*, 2017). We followed the taxonomy of the May 2021 Reptile Database (http://www.reptile-database.org/) (Uetz *et al.*, 2021) and the checklists of reptiles of China (Wang *et al.*, 2020).

We added the 212 species ranges to three scaled grids (large scale: 1.5° × 1.5°, medium scale: 1° × 1°, and small scale: 0.5° × 0.5°) using the "letsR" package (Vilela and Villalobos, 2015) and calculated the species numbers in each grid. We excluded grid cells with less than 60% land cover owing to the national boundary and coastline. Finally, we removed 100, 109, and 240 grids, respectively. The species richness pattern of lizards driven

by climate may differ among the insular and mainland regions (e.g., anolis lizards, Velasco *et al.*, 2018). One important study on Chinese lizard species richness excluded all island grids to avoid the effects of insularity (Huang *et al.*, 2011); here we kept all island grids and performed analyses with and without them to explore the influence of insularity (see below).

We used nine climatic factors based on previous studies (Huang *et al.*, 2011; Qian *et al.*, 2007; Zhao *et al.*, 2006) to explore the climate–species richness (five hypotheses, also see Table 1) relationships within scales. Specific, (1) Ambient energy: The mean annual temperature; (2) Water-energy dynamic: annual precipitation; (3) Seasonality: temperature seasonality, and precipitation seasonality; (4) Productivity: net primary productivity (NPP) and the actual evapotranspiration (AET); (5) Heterogeneity: Altitude range and standard deviation (SD). We noted that all five climatic data were obtained from high-resolution climatologies (1901–2016) at high resolution for the earth's land surface areas (CHELSA; http://chelsa-climate. org/), whereas the NPP data were obtained from the Moderate Resolution Imaging Spectroradiometer database (MODIS; http://www.ntsg.umt.edu/project/mod17). The AET data was taken from Trabucco and Zomer (2010), and the altitude data was obtained from http://edcintl.cr.usgs.gov. We calculated the altitudinal range using the highest altitude minus the lowest altitude of each grid, and we further calculated the standard deviation (SD) of the altitude of each grid (Table 1).

**2.2. Data analysis** We first computed species richness–latitude regressions to determine if each scale exhibited similar latitudinal richness gradient. We tested the residuals for spatial autocorrelation with Moran's Ι correlograms (the 'pgirmess' R package, Giraudoux, 2018). Then, we explored the relationship between species richness and altitude using generalized additive models (GAM, mgcv package, Wood, 2017). We further regarded latitude as a factor in the GAMs to account for the latitudinal gradients of species richness.

We performed multiple spatial autoregressive (SAR) models (Dormann *et al.*, 2007) to account for spatial autocorrelation. We used species richness as the response variable, and the nine environmental variables as predictors (*errorsarlm* function in the "spdep" package) (Bivand and Wong, 2018) to explore the relationships between richness and climatic factors. All analyses were performed within the three scales with and without island grids to explore whether insularity would affect the climate–species richness relationships.

Repeated species co-occurrences could generate unreliable relationships between richness and climate (Hawkins *et al.*, 2017), and thus indicate a departure from actual relationships. Consequently, we used a null modeling approach by randomizing richness among grid cells and generating 100 random lizard richness gradients. Modeling of these 100 randomized richness gradients was performed using the aforementioned SAR models and we further evaluated the difference between the observed and 100 random Nagelkerke pseudo-$R^2$ values based on single-sample *t*-tests. If the 100 random Nagelkerke pseudo-$R^2$ values were significantly lower than the observed values, we considered the observed pattern to be reliable (Hawkins *et al.*, 2017). Lizard species richness and climates were $log_{10}$-transformed. Statistical tests were performed using R software (R core team, 2019). We also used the packages "raster", "maps", "spatialreg" (Bivand *et al.*, 2013; Bivand and Wong, 2018; Hijmans, 2020).

## 3. Results

There were 415, 980, and 3889 grid cells at the large (1.5°), medium (1°), and small (0.5°) scales, respectively; with all island cells removed, these numbers changed to 411, 976, and 3879, respectively. The richness of each grid varied from 2 to 47, 1 to 46, and 1 to 44 at the large, medium, and small scales, respectively. Lizards with high richness (species richness ≥ 30) were the major inhabitants in south China (e.g., Guangxi,

**Table 1** All nine environmental variables included in our study, with their abbreviations and hypotheses.

| Variables | Abbreviations | Hypotheses | References |
|---|---|---|---|
| Annual Mean Temperature | Tem | Ambient energy. Energy availability generates and maintains richness gradients. | Evans *et al.*, 2005 |
| Annual Precipitation | Pre | Water–energy dynamic. Water–energy dynamic could shape species richness pattern at a large scale. | Evans *et al.*, 2005; Hawkins *et al.*, 2003 |
| Temperature Seasonality | TS | Seasonality. Regions with lower seasonality could have more species than those with higher seasonality. | Klopfer, 1959; Gouveia *et al.*, 2013 |
| Precipitation Seasonality | PS | | |
| Net primary productivity | NPP | Productivity. Regions with higher productivity could have more species than those with lower productivity. | Evans *et al.*, 2005 |
| Actual Evapotranspiration | AET | | |
| Altitude | Altitude | Heterogeneity. Regions with more complex habitats could have more species than those with less complex habitats. | Rahbek and Graves, 2001 |
| Altitude Range | Altitude R | | |
| Altitude standard deviation | Altitude SD | | |

Guangdong, Hainan, and Taiwan provinces), whereas those with low richness (species richness ≤ 5) were mainly found on the Qinghai–Tibet Plateau and in northeast China.

We found an effect of latitude on species richness across Chinese lizards ($P < 0.001$ at all three scales; Figure 2A, B, C). Residual spatial autocorrelations (Moran's Ⅰ index) were less than 0.5 for all three scales (Figure 2D, E, F).

We found a new species richness–altitude pattern, based on all three scales, in which the lizard richness decreased with increasing altitude when the altitude was less than 600 m, increased with increasing altitude from 600 to 2500 m, and decreased at altitudes above 2500 m (Figure 3A, B, C cf. Figure

1). However, we found a low-altitude plateau pattern between the species richness and altitude ($P < 0.001$ in all cases) at all three scales when we accounted for the latitude. Additionally, the lizard richness decreased at altitudes above 2500 m (Figure 3D, E, F).

Multiple SAR models revealed that multiple climatic variables explained the spatial patterns of Chinese lizard species richness at all three scales. For example, temperature and NPP were positively correlated with lizard richness, while seasonality (both temperature and precipitation) and AET were negatively correlated with lizard richness. We further found that some determinants of lizard richness varies among the
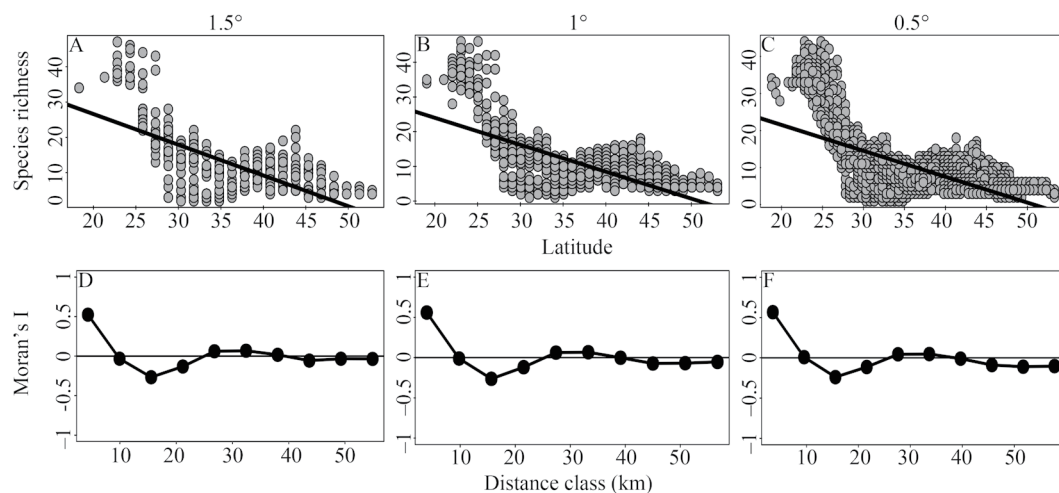


**Figure 2** Latitudinal richness gradient of lizards at 1.5° × 1.5° (A), 1° × 1° (B), and 0.5° × 0.5° (C) scales. Residual spatial autocorrelogram for the lizard latitudinal richness gradients at 1.5° × 1.5° (D), 1° × 1° (E), and 0.5° × 0.5° (F) scales.
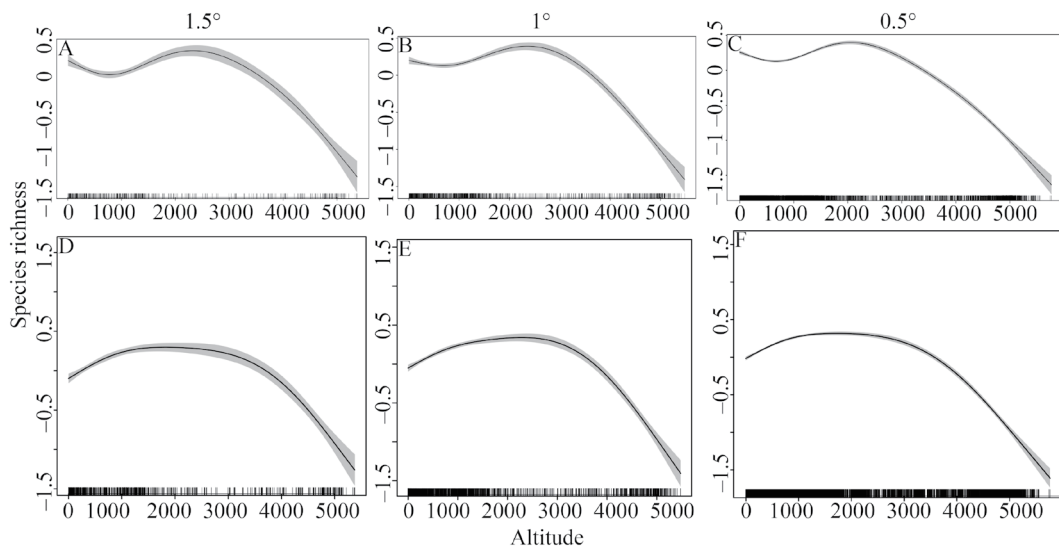


**Figure 3** Spatial gradients of species richness with altitude among Chinese lizards. A, D: 1.5° × 1.5°; B, E: 1° × 1°; and C, F: 0.5° × 0.5°.

different scales, e.g., precipitation was positively correlated with richness only at the large scale, and altitudinal SD was positively correlated with richness only at the medium scale (Table 2). The results of environmental factors — species richness correlations were similar when with and without all island grid cells, expect for precipitation at the large scale, which was no longer positively correlated with richness ($P > 0.05$) when removing island grids (Table 2). The null model approach performed here revealed that the observed Nagelkerke pseudo-$R^2$ values were significantly larger than the random values (Table 2 cf. Appendix S2). We therefore considered that the detected richness–climate correlations were reliable, and environmental variables indeed can influence the observed species richness pattern across Chinese lizards.

## 4. Discussion

We found that the latitudinal diversity gradient of Chinese lizards with species richness decreased with increasing latitude, whereas the relationship between the species richness and altitude showed a low-altitude plateau pattern overall. We further found that the determinants of the spatial patterns of Chinese lizard richness varied slightly within different scales. In agreement with previous studies (Huang *et al.*, 2011; Qian *et al.*, 2007; Zhao *et al.*, 2006), the spatial patterns of Chinese lizard species richness were driven by multiple factors.

Many studies have focused on species richness patterns and their determinants on a single scale (Dillon and Conway, 2021; Pontarp *et al.*, 2019; Whiting and Fox, 2021), and few have focused on multiple scales (but see Evans *et al.*, 2008). Different scales contain different levels of climate heterogeneity within grids. Thus, the degree of correlation between richness patterns and determinants may vary within different scales. The determinants of richness patterns could also differ among scales (Field *et al.*, 2010). For example, Rodríguez *et al.* (2005) found that annual potential evapotranspiration and temperature drive

reptile richness at a large scale, while Whittaker *et al.* (2007) found a strong correlation between precipitation and reptile richness at a small scale.

In the current study, we found that two determinants of lizard richness pattern varied within different scales. First, precipitation was positive correlated with lizard richness only at the large scale. However, we did not detect significant correlation between precipitation and lizard richness after we omitted the island grids. This suggested that the correlation between lizard richness and precipitation is influenced by insularity at the largest scale (1.5°). Precipitation is a stronger predictor for ectotherms—especially amphibians because they need water to keep their skin wet—than for endotherms (Pincheira-Donoso *et al.*, 2019; Whittaker *et al.*, 2007). Lizard richness, however, is rarely correlated with precipitation (Schall and Pianka, 1978). This is because they are adapted to arid environments (Powney *et al.*, 2010), and do not rely on water to keep their skin wet. Indeed, arid regions (northwest China) is not the lowest region of lizard richness in this study. Moreover, the distribution of amphibians and reptiles in the arid regions of China is influenced by a combination of climatic and geographical factors, not just one factor (Zhou, 2019). Therefore, we concluded that precipitation cannot predict the richness patterns of Chinese lizards.

Second, the altitudinal SD was correlated with lizard richness at a medium scale, and this result was consistent after we removed the island grids. This suggests that lizard richness increases with increasing altitude heterogeneity, which is consistent with the prediction of heterogeneity (Rahbek and Graves, 2001). In southwest China, the Hengduan Mountains region has a complex environment, and produces a high diversity of both species and ecological regions (Zhang *et al.*, 2021) for lizards to inhabit. Although the Pamirs and Qinghai–Tibet Plateau in western China have high altitudes, their altitudinal heterogeneity and climatic diversity are low, and their species richness is not high, which is consistent with our

**Table 2** Multiple spatial autoregressive (SAR) model results of relationships between lizard richness and climate among Chinese lizards with (A) and without (B) island grid cells.

| Scale | Tem | Pre | TS | PS | AET | NPP | Altitude R | Altitude SD | Altitude | $R^{2*}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| A | | | | | | | | | | |
| 1.5 | **0.63±0.1**\*\* | **0.13±0.06**\* | **−0.69±0.14**\* | **−0.36±0.09**\*\*\* | **−0.36±0.07**\*\*\* | **0.21±0.03**\*\*\* | −0.03±0.06 | 0.08±0.05 | 0.01±0.02 | 0.84 |
| 1 | **0.59±0.06**\*\*\* | 0.07±0.04 | **−0.73±0.98**\*\*\* | **−0.31±0.06**\*\*\* | **−0.34±0.04**\*\* | **0.21±0.02**\*\*\* | −0.04±0.04 | **0.08±0.04**\* | −0.01±0.02 | 0.83 |
| 0.5 | **0.56±0.03**\*\*\* | 0.03±0.02 | **−0.83±0.05**\*\*\* | **−0.33±0.03**\*\*\* | **−0.29±0.02**\*\*\* | **0.19±0.01**\*\*\* | 0.001±0.02 | 0.04±0.02 | −0.01±0.01 | 0.81 |
| B | | | | | | | | | | |
| 1.5 | **0.61±0.1**\*\* | 0.12±0.06 | **−0.91±0.15**\*\*\* | **−0.39±0.09**\*\*\* | **−0.39±0.07**\*\*\* | **0.21±0.03**\*\*\* | −0.04±0.06 | 0.08±0.05 | −0.003±0.03 | 0.84 |
| 1 | **0.59±0.06**\*\*\* | 0.07±0.04 | **−0.77±0.1**\*\*\* | **−0.32±0.06**\*\*\* | **−0.35±0.05**\*\*\* | **0.2±0.02**\*\*\* | −0.04±0.04 | **0.08±0.04**\* | −0.01±0.02 | 0.83 |
| 0.5 | **0.55±0.03**\*\*\* | −0.03±0.02 | **−0.83±0.05**\*\*\* | **−0.33±0.03**\*\*\* | **−0.29±0.02**\*\*\* | **0.19±0.01**\*\*\* | 0.001±0.02 | 0.04±0.02 | −0.01±0.01 | 0.81 |

* Nagelkerke's pseudo-R2, but these cannot be interpreted as the percentage of variance explained by the model.

results. Different scales contain different levels of altitudinal heterogeneity within grids. This may lead to the heterogeneity hypothesis not being supported at the small and large scales.

We found a new pattern of altitudinal gradients of richness in this study. In regions where the altitude was less than 600 m (mainly in eastern China), the lizard richness decreases with increasing latitude and altitude, lizard richness increased with increasing altitude from 600 to 2500 m, and decreased at altitudes above 2500 m. To our knowledge, such a pattern has not been observed before with regard to altitudinal gradients of species richness (this study cf. McCain, 2010). However, this new pattern was no longer supported after we considered the latitude. Because we further found a low-altitude plateau pattern when accounting for latitude, where lizards maintained a high richness at altitudes of less than 2500 m. This suggests that the relationship between species richness and altitude was influenced by latitude. However, the lizard richness decreased with increasing altitude from 600 to 2500 m. This may be because more species inhabit the Hengduan Mountains owing to their complex environments (see above). At the same time, this region is at a low latitude, with high temperatures and shorter seasonality (see below). High altitudinal heterogeneity creates complex habitats and varying degrees of isolation, which in turn affects evolutionary diversity. At the same time, this habitat diversity also produces many transition zones between different environments, where species richness is usually high (Zhou and Shi, 2015).

We found evidence of a low-altitude plateau in Chinese lizard richness overall. However, at the local scale, multiple altitudinal species richness patterns existed. For example, reptile richness decreases with increasing altitude in the Altay prefecture (Tao et al., 2018), this pattern also hold in tropical lizards (Jins et al., 2021), whereas Zheng et al. (2014) found that reptile richness followed a mid-altitude peak in the Qinling range. Altitudinal gradients of species richness are influenced by multiple variables (Dillon and Conway, 2021; McCain, 2010). Therefore, the overall pattern may not be informative in exploring the altitudinal gradients of Chinese lizard richness (also see Ignacio et al., 2018).

In agreement with Qian et al. (2007), we also found that temperature was positively correlated with lizard richness in this study. Ectotherms (e.g., lizards) are more closely associated to ambient energy (Hawkins et al., 2003; McCain, 2010; Rodríguez et al., 2005), and energy variability controls species richness. This may explain the latitudinal species richness gradient (i.e., species richness decreases with increasing latitude) of lizards across China.

Previous studies have suggested that productivity is associated with species richness (Lewin et al., 2016). Both AET and NPP can represent productivity (Huang et al., 2011),

However, we suggest that NPP is more representative of productivity than AET is in this study. We found that Chinese lizard richness increased with increasing NPP but decreased with increasing AET at all three scales. Lizard richness was the greatest in south China. The northward decrease in lizard richness in China is likely to be related to a decrease in productivity; however, the potential mechanism of this is still unknown. Productivity as a main drive of lizard richness spatial patterns could perhaps be related to insects (e.g., birds, Dalby et al., 2014); regions with sparse vegetation might provide fewer insects and, hence, have fewer species of lizard. This suggested that NPP is a stronger predictor for Chinese lizard richness than AET is.

The seasonality hypothesis proposes that species richness decreases with increasing seasonal variability (Gouveia et al., 2013; Rahbek, 1995). Here, we found that lizard richness decreased with increasing seasonality, which is consistent with the seasonality prediction. This correlation seems to be associated with both NPP and the ambient energy hypotheses; increased seasonality may increase the variation in productivity (and energy) and, hence, reduce species richness (Evans et al., 2005, also see above). Furthermore, species inhabiting low richness regions could have wider distributions, promoting the evolution of climatic tolerances and enabling species to breed over larger areas (Evans et al., 2005; Slobodkin and Sanders, 1969).

Large-scale richness patterns are driven by the complexity of multiple factors, such as evolutionary and ecological factors (Velasco et al., 2018), and the overall patterns may be different across taxa (Liang et al., 2021). Moreover, rapid global climate change may influence the distribution and diversity patterns of species. We did not test this in this study. However, this should be performed in a future study to help face the challenges imposed by climate change on the Chinese lizard population.

## 5. Conclusions

We demonstrated that both the latitudinal and altitudinal gradients of Chinese lizard richness varied slightly within different scales. The species richness patterns of Chinese lizards were consistent with the predictions of the ambient energy, seasonality, and productivity hypotheses across multiple scales. Altitudinal gradients of lizard richness patterns were influenced by latitude. The relationship between lizard richness and habitat heterogeneity however differed among the studied scales in Chinese lizards.

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## Appendix S1

**List of the 212 species used in the analysis**

**GEKKONIDAE:** *Hemiphyllodactylus typus, Hemiphyllodactylus changningensis, Hemiphyllodactylus dushanensis, Hemiphyllodactylus huishuiensis, Hemiphyllodactylus jinpingensis, Hemiphyllodactylus longlingensis, Hemiphyllodactylus hongkongensis, Hemiphyllodactylus yunnanensis, Gekko scabridus, Gekko gecko, Gekko japonicus, Gekko auriverrucosus, Gekko kwangsiensis, Gekko guishanicus, Gekko similignum, Gekko reevesii, Gekko kikuchii, Gekko liboensis, Gekko melli, Gekko subpalmatus, Gekko hokouensis, Gekko taibaiensis, Gekko wenxianensis, Gekko swinhonis, Gekko adleri, Gekko chinensis, Gehyra mutilate, Lepidodactylus lugubris, Lepidodactylus yami, Altiphylax stoliczkai, Cyrtodactylus cayuensis, Cyrtodactylus wayakonei, Cyrtodactylus tibetanus, Cyrtodactylus zhaoermii, Alsophylax przewalskii, Alsophylax pipiens, Ptychozoon bannaense, Cyrtopodion medogense, Hemidactylus garnotii, Hemidactylus brookii, Hemidactylus aquilonius, Hemidactylus stejnegeri, Hemidactylus platyurus, Hemidactylus frenatus, Hemidactylus bowringii, Tenuidactylus dadunensis, Tenuidactylus elongatus, Mediodactylus russowii.*

**SHINISAURIDAE:** *Shinisaurus crocodilurus.*

**EUBLEPHARIDAE:** *Goniurosaurus bawanglingensis, Goniurosaurus kwangsiensis, Goniurosaurus hainanensis, Goniurosaurus kadoorieorum, Goniurosaurus lichtenfelderi, Goniurosaurus liboensis, Goniurosaurus luii, Goniurosaurus yingdeensis, Goniurosaurus Araneus, Goniurosaurus zhelongi, Goniurosaurus sinensis, Goniurosaurus zhoui.*

**VARANIDAE:** *Varanus nebulosus, Varanus irrawadicus, Varanus salvator.*

**AGAMIDAE:** *Trapelus sanguinolentus, Draco maculatus, Draco blanfordii, Ptyctolaemus gularis, Acanthosaura lepidogaster, Acanthosaura tongbiguanensis, Acanthosaura armata, Leiolepis reevesii, Diploderma batangense, Diploderma flaviceps, Diploderma brevicaudum, Diploderma brevipes, Diploderma vela, Diploderma iadinum, Diploderma slowinskii, Diploderma fasciatum, Diploderma laeviventre, Diploderma varcoae, Diploderma splendidum, Diploderma polygonatum, Diploderma dymondi, Diploderma micangshanense, Diploderma chapaense, Diploderma swild, Diploderma swinhonis, Diploderma zhaoermii, Diploderma makii, Diploderma graham, Diploderma luei, Diploderma yulongense, Diploderma yunnanense, Diploderma drukdaypo, Pseudocalotes kakhienensis, Pseudocalotes brevipes, Pseudocalotes austeniana, Pseudocalotes kingdonwardi, Pseudocalotes microlepis, Japalura andersoniana, Japalura tricarinata, Phrynocephalus versicolor, Phrynocephalus mystaceus, Phrynocephalus putjatai, Phrynocephalus helioscopus, Phrynocephalus melanurus, Phrynocephalus erythrurus, Phrynocephalus przewalskii, Phrynocephalus nasatus, Phrynocephalus forsythia, Phrynocephalus grumgrzimailoi, Phrynocephalus vlangalii, Phrynocephalus theobaldi, Phrynocephalus axillaris, Phrynocephalus alpherakii, Calotes emma, Calotes mystaceus, Calotes versicolor, Calotes jerdoni, Calotes medogensis, Calotes Paulus, Laudakia sacra, Laudakia tuberculate, Laudakia wui, Laudakia papenfussi, Laudakia himalayana, Laudakia stoliczkana, Physignathus cocincinus.*

**SPHAERODACTYLIDAE:** *Teratoscincus roborowskii, Teratoscincus przewalskii, Teratoscincus scincus.*

**ANGUIDAE:** *Dopasia harti, Dopasia hainanensis, Dopasia gracilis.*

**SCINCIDAE:** *Sphenomorphus maculatus, Sphenomorphus tonkinensis, Sphenomorphus incognitus, Sphenomorphus courcyanum, Sphenomorphus taiwanensis, Sphenomorphus indicus, Emoia atrocostata, Ablepharus alaicus, Ablepharus deserti, Ateuchosaurus chinensis , Scincella huanrenensis, Scincella potanini, Scincella barbouri, Scincella ladacensis, Scincella reevesii, Scincella modesta, Scincella tsinlingensis, Scincella monticola, Scincella formosensis, Scincella schmidti, Scincella przewalskii, Scincella sikimmensis, Scincella himalayanus, Scincella doriae, Tropidophorus berdmorei, Tropidophorus guangxiensis, Tropidophorus hainanus, Tropidophorus sinicus, Eutropis multicarinata, Eutropis multifasciata, Eutropis cumingi, Eutropis longicaudata, Plestiodon leucostictus, Plestiodon popei, Plestiodon tunganus, Plestiodon capito, Plestiodon elegans, Plestiodon liui, Plestiodon quadrilineatus, Plestiodon tamdaoensis, Plestiodon chinensis, Lygosoma bowringii.*

**DIBAMDAE:** *Dibamus bourreti, Dibamus bogadeki.*

**LACERTIDAE:** *Takydromus wolteri, Takydromus septentrionalis, Takydromus sylvaticus, Takydromus viridipunctatus, Takydromus intermedius, Takydromus kuehnei, Takydromus amurensis, Takydromus sauteri, Takydromus luyeanus, Takydromus sexlineatus, Takydromus stejnegeri,*

*Takydromus formosanus, Takydromus albomaculosus, Takydromus hsuehshanensis, Takydromus yunkaiensis, Eremias arguta, Eremias vermiculata, Eremias przewalskii, Eremias buechneri, Eremias kokshaaliensis, Eremias velox, Eremias argus, Eremias multiocellata, Eremias yarkandensis, Eremias brenchleyi, Eremias quadrifrons, Eremias stummeri, Eremias roborowskii, Eremias grammica, Zootoca vivipara, Lacerta agilis.*

# Appendix S2

## Results of *t*-test between $R^2$ values

| | Mean | *t* | *P* |
|---|---|---|---|
| Middle with islands | 0.013 | −1502.6 | <0.001 |
| Middle without islands | 0.013 | −1287.2 | <0.001 |
| Big with islands | 0.03 | −675.33 | <0.001 |
| Big without islands | 0.03 | −608.81 | <0.001 |
| Small with islands | 0.003 | −6085.7 | <0.001 |
| Small without islands | 0.003 | −5473.8 | <0.001 |